

TAXONOMY AND DISTRIBUTION OF
GENTIANA (GENTIANACEAE) IN MEXICO
AND CENTRAL AMERICA. II. SECT.
*CHONDROPHYLLAE*¹

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This paper is the second of two monographs on *Gentiana* L. in Mexico and Central America. Delineation of the genus, terms pertaining to its morphology, and other introductory topics were discussed in the first paper (Pringle 1977), which also included a key to the sections of *Gentiana* in these regions.

GENTIANA [sect.] *CHONDROPHYLLAE* Bunge, *Nouv. Mém. Soc. Imp. Naturalistes Moscou* 1:207. 1829. Lectotype species (Pringle 1978): *Gentiana aquatica* L.

Varasia Philippi, *Florula Atacamensis* p. 35. 1860. Type species (only species cited): *Gentiana podocarpa* (Philippi) Griseb., as *Varasia podocarpa* Philippi. *Chondrophylla* (Bunge) A. Nels., *Bull. Torrey Bot. Club* 31:245. 1904 (pro gen.).

Holubia Löve & Löve, *Anales Inst. Bot. Cavanilles* 32:226. 1975. Type species: *Gentiana pyrenaica* L., as *Holubia pyrenaica* (L.) Löve & Löve. Non *Holubia* Oliver, *Hooker's Icon. Pl.* 15:59. 1884.

Holubogentia Löve & Löve, *Bot. Not.* 131:385. 1978. Based on *Holubia* Löve & Löve, non Oliver.

Plants monocarpic or perennial. Roots slender, branched; taproot persistent in annual species. Stems solitary or clustered, usually branched except in minute plants, decumbent to erect, slender, in many species less than 15 cm long, up to 30 cm in others. Basal and lower cauline leaves of most monocarpic and some perennial species persistent, crowded, and broader than median and upper cauline leaves. Leaf bases strongly connate-sheathing. Blades usually less than 1.5 cm long, scalelike to oblanceolate, oblong, or orbicular, usually carinate. Margins obscurely to prominently white-cartilaginous, entire or minutely denticulate. Flowers solitary or in small, condensed cymes, without involucrel bracts, 5–30 mm long. Calyx tubes 5- or 15-veined, cylindrical to funnellform, unclft. Calyx lobes deltoid to oblong, often carinate, with cartilaginous margins. Intracalycular membrane discontinuous or not developed. Corollas usually pale to deep blue, sometimes white, pale yellow, or violet, usually suffused externally with green and/or deep violet, often

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photo-, thigmo-, and seismonastically closing. Corolla tubes cylindrical to funnelliform. Corolla lobes abruptly wide-spreading, shorter than tube, deltoid to ovate or oblong-ovate. Free portions of corolla appendages nearly symmetrical, unclenched to shallowly or deeply bifid, or erose to fimbriate. Stamens equal, with straight filaments. Anthers free or loosely connate. Pollen grains oblate-spheroidal to prolate. Sexine striate, striato-reticulate, or nearly smooth. Ovaries compressed-ellipsoid, usually widest near middle, abruptly contracted at summit. Stigmas short, in most species sessile or subsessile, in some elevated by a well-developed style. Gynophores of some species greatly elongating in fruit, remaining short in others. Carpels each with 1 dorsal and 2 ventral veins. Ovules in 4 parietal zones corresponding to positions of ventral carpel veins. Seens ovoid to ellipsoid, often apiculate, wingless or with narrow, incomplete wings. Testa striato-reticulate. Sectional description compiled from Kusnezov (1895), Lindsey (1940), Nilsson (1967), Toyokuni (1963), and my own observations.

Section *Chondrophyllae* occurs in the Pyrenees, the Alps, and the Carpathians; in the Caucasus, the Himalayas, Siberia, China, Japan, and Southeast Asia; in Indonesia, New Guinea, and the Philippines; from the Aleutians and the Brooks Range in Alaska through the Rocky Mountains to Arizona; in Mexico, Guatemala, and Costa Rica; and in the Andes from Venezuela to Tierra del Fuego. Throughout its range, this section is confined largely to mountainous regions, with many of its species occurring above treeline.

The pollination of *G. prostrata* Haenke in Europe has been discussed by Kerner von Marilaun (1891), who concluded that although outcrossing was promoted by protandry, autogamy could readily occur within corollas prevented from opening by prolonged cloudy periods. Similarities in corolla morphology and in pistil and anther development indicate that these conclusions are generally applicable to the species discussed in the present paper. The widespread phenomenon of thigmonastic corolla-closing in this section is usually assumed to be related to pollination, but its specific role has not been investigated.

From the field aspect of open capsules of *G. perpusilla* Brandege, it appears that the fruits of this and some other species of sect. *Chondrophyllae* function as splash-cups. In species with more elongate gynophores, seeds are probably dispersed as wind shakes the fruits (censer mechanism). Many species grow where rill action can further disperse the seeds after they have fallen. Long-distance dispersal evidently has also occurred, since the alpine habitats of the Mexican and Central American species are widely separated, are mostly of late Tertiary or Quaternary origin, and have no history of connection by continuous alpine vegetation.

Since its establishment by Bunge, sect. *Chondrophyllae* has been accepted as a section of *Gentiana* by most authors, except for those who restricted *Gentiana* to the five species usually treated as its nominate section. *Varasia* Philippi and *Chondrophylla* (Bunge) A. Nels. were equivalent to sect.

Chondrophyllae only. Neither of these names has been used recently.

Löve & Löve (1975) divided sect. *Chondrophyllae* between two segregate genera. The "annual or biennial species with $x = 9$ " were placed, along with sect. *Ciminalis* (Adans.) Dumort. (which consists of perennial species), in the genus *Ciminalis* Adans. emend. Holub (type species: *Gentiana acaulis* L., in sect. *Ciminalis*, as *Ciminalis* [sp.]). The "perennial species . . . with . . . $x = 13$," believed by Löve & Löve to comprise "about ten species of Eurasia, North and South America," formed *Holubia* Löve & Löve, later renamed *Holubogentia* Löve & Löve. Weaver & Rüdénberg (1975), however, reported $n = 20$ in plants called *G. sedifolia*, but probably an unnamed, closely related species, in Venezuela. In Löve & Löve's generic concept, this species, perhaps with certain Asiatic species having $n = 10$, will presumably be treated as a third genus.

Little can now be postulated about relationships within sect. *Chondrophyllae* in the Western Hemisphere, because its diversity has largely remained unrecognized. Existing information on chromosome numbers and pollen morphology indicates that phylogenetic studies will require more such data. Subdivisions of sect. *Chondrophyllae* are therefore not considered here.

In this study, I examined specimens in the following herbaria: BM, DS, ENCB, F, GH, HAM, K, MEXU, MICH, MO, MSC, NY, TENN, US, and WIS (abbreviations from Holmgren & Keuken 1974). Among these are collections each comprising several to many plants, representing well the variation that may occur within a population. Specimens from South America, northern North America, and Eurasia were among those studied, and *G. perpusilla* and *G. prostrata* were observed in the field. Consequently, it has been possible to compare the Mexican and Central American plants with those in other regions, and to distinguish, with reasonable confidence, taxonomically significant differences among populations from minor variations among individuals.

All of the species discussed here have sometimes been equated with *G. prostrata*. Comparisons with specimens of *G. prostrata* from Colorado (Figs. 7, 13), Alaska (Fig. 19), and the type region in Austria, however, indicate that all of the Mexican and Central American plants are distinct from this species. *Gentiana fieldiana*, which resembles *G. prostrata* in its leaf shape and in its apiculate corolla lobes, differs in its wider white leaf margins, in the more oblong shape and strict apical symmetry of its corolla lobes, in the greater adnation of its stamens, and in its usually cymose inflorescences. *Gentiana sedifolia* resembles *G. prostrata* in its narrow leaf margins and in the long free portions of its filaments, but differs in its proportionately much narrower leaves, in its blunt corolla lobes, in its more copiously and more irregularly erose-serrate corolla appendages, and in its coarser sexine sculpturing without well-developed longitudinal striations. The other species differ even more sharply from *G. prostrata*: *G. beamanii* in its narrower leaves and in the much shorter free portions of its stamens, *G. perpusilla*

in its proportionately small corolla lobes and in its unclift, nearly entire corolla appendages, and *G. pumilio* in its proportionately much broader leaves, in its wide and prominently denticulate leaf margins, and in its spheroidal pollen grains.

KEY TO MEXICAN AND CENTRAL AMERICAN SPECIES

- 1a. Leaves imbricately crowded, broadly spatulate to orbicular, many with 5 or more prominent primary veins and 2-4 lesser ones; white leaf margins conspicuous, ca. 0.3 mm wide, those of upper leaves denticulate from below middle to apex; flowers often sessile in small clusters; calyx tube largely concealed by leaves; pollen grains spheroidal 4. *G. pumilio*
- 1b. Leaves, except sometimes near base of stem, less densely crowded and proportionately narrower, usually with only 1 or 3 prominent primary veins; white leaf margins 0.2 mm or less in width, entire or denticulate above middle; flowers solitary at end of main stems and branches; calyx tube not concealed; pollen grains subprolate to prolate.
- 2a. Leaves linear-oblong, usually more than 3 times as long as wide, slightly to strongly divergent from near base; stamens becoming free in lower 2/5 of corolla, with free portions, including anthers, 3-7 mm long; throat of corolla with distinct color demarcation 1. *G. sedifolia*
- 2b. Leaves oblanceolate to obovate, usually less than 3 times as long as broad, if proportionately longer then proximally appressed-ascending, only the distal portion spreading; stamens becoming free near or above middle of corolla, with free portions up to 3 mm long, or, if diverging lower, then with free portions up to 2 mm long and with corolla appendages subentire; throat of corolla with or without color differentiation.
- 3a. Stems erect except at base, with strongly ascending branches; internodes, except near base of stem, mostly as long as or longer than subtending leaves; leaf blades mostly over 5 mm long; throat of corolla with distinct markings 2. *G. beamanii*
- 3b. Stem and branches variously spreading; internodes mostly much shorter than subtending leaves; many leaf blades less than 5 mm long; corolla throat paler but neither sharply demarcated nor streaked.
- 4a. White leaf margins and keel well defined, those of upper leaves distinctly denticulate; corolla lobes oblong-triangular, abruptly rounded to apiculate tip; free portions of corolla appendages erose-serrate; stamens becoming free near middle of corolla 3. *G. fieldiana*
- 4b. White leaf margins and keel obscure, generally entire or shallowly undulate; corolla lobes ovate-triangular, tapering gradually to subacute tip; free portions of corolla appendages entire or nearly so; stamens becoming free below middle of corolla 5. *G. perpusilla*

TAXONOMIC TREATMENT

1. GENTIANA SEDIFOLIA H.B.K., Nov. Gen. Sp. Pl. 3:173. 1819 (quarto text). Type: without locality [probably ECUADOR: Napo or Pichincha]: *Humboldt & Bonpland s.n.*, no date [probably Jan-Jun 1802] (holotype P, photo MSC! isotype K!). Figs. 1, 8, 14.

Gentiana cespitosa Willd. ex Schultes, Syst. Veg. 6:185. 1820. Type: Duplicate *Humboldt et al.*, cited above (B-herb. Willd.). (Ex char. and fide Kunth in

Humboldt et al., 1823.)

Gentiana chimboracensis Willd. ex Schultes, Syst. Veg. 6:185. 1820. Type: ECUADOR: Chimborazo: Chimborazo, *Humboldt et al. s.n.*, no date (B-herb. Willd.). (Ex char.)

Ericala sedifolia (H.B.K.) G. Don, Gen. Hist. 4:189. "1838" [1837].

Gentiana edifolia var. *casapaltensis* J. Ball, J. Linn. Soc., Bot. 22:49. 1885. Type: PERU: Lima: supra Casapalta [Casapalca], *Ball s.n.*, 22 Apr 1882 (holotype K! isotype GH!).

Gentiana sedifolia var. β *grandiflora* Kusn., Trudy S.-Peterburgsk. Obshch. Estestvoisp., Otd. Bot. 24(2):217. 1894. Syntypes: ECUADOR: Napo or Pichincha: Antisana, *Lebmann*, no. and date not cited (LE) and COLOMBIA: Magdalena: Santa Marta, *Lebmann*, no. and date not cited (LE); probable isosynotype, "Cordillera of Ecuador and Colombia," *Lebmann* 623, 22 Dec 1880 (K!).

Plants usually 1.3–4 cm tall, occasionally up to 6 cm. Stems 1-many. Well-developed stems decumbent at least at base and often for much of length; longer stems usually much branched. Leaves linear-oblong, 5–10 mm long, 1.5–2.5 (–3) mm wide, apiculate. White leaf margins inconspicuous and sometimes not sharply defined, mostly 0.02–0.06 mm wide distally on lower leaves, ca. 0.1 mm wide on upper leaves, entire or irregularly and minutely denticulate toward apex. Basal leaves persistent, crowded, less conduplicate than cauline leaves. Cauline leaves increasingly conduplicate and sometimes more or less arcuate on upper part of stem (except on very small plants), with midrib keels more distinctly developed (white portions up to 0.05 mm wide). Median and upper internodes often scarcely longer than sheathing leaf bases, sometimes up to 2–6 mm long. Calyx tube 5.5–8 mm long, ridged distally along median sepal veins. Calyx lobes ovate-triangular, erect proximally, sometimes more or less arcuate distally, conduplicate and narrowly carinate toward apex, (1.2–)1.8–4 mm long, acute, with white margins ca. 0.2 mm wide, widening near apex, and keel up to 0.05 mm wide; margins and keel entire. Corollas 9–20 mm long when closed; expanded limb 6–14 mm across. Corolla tube 6.5–17 mm long. Lobes broadly ovate-triangular, 1.8–4 mm long, as wide or slightly wider than long, obtuse to subacute. Free portions of appendages ca. 0.75 times as long and about as wide as lobes, broadly rounded to triangular, shallowly to rather deeply erose-serrate or shallowly several-cleft near apex, not distinctly bifid. Corolla tube yellowish-white; upper portion suffused with deeper yellow and often bordered and spotted with purplish-brown. Uppermost part of fused portion of corolla, lobes, and free portion of appendages pale to deep blue, with a narrow whitish zone next to yellowish eye, or occasionally yellowish-white throughout; exterior surface of lobes, except near inner margin, and adjacent portions of tube suffused with deep violet (scarcely or not at all in white-flowered forms) and also with green, especially near tips of lobes. Stamens becoming free at 1/4–2/5 total height of corolla; free portions (including anthers) 3–7 mm long. Pollen grains prolate. Sexine relatively coarsely striato-reticulate. Pistil tapering into style ca. 1 mm long. Capsule 3–5 mm



Figs. 1-3. Herbarium specimens of *Gentiana* spp. Fig. 1. *G. sedifolia* (Mulroy 1099, HAM, from Ecuador). Fig. 2. *G. beamanii* (Beaman 3899, MSC). Fig. 3. *G. fieldiana* (Beaman 3071, MSC, a relatively large plant).

long, elevated well above marcescent corolla by gynophore 15–18 mm long at maturity. Seeds ellipsoid, light brown, striato-reticulate, ca. 0.85 mm long, 0.4 mm in diameter.

Central American specimens examined:

COSTA RICA: Cartago (all from Cordillera de Talamanca, near Cerro de la Muerte): not more specifically located, *Carlson* 3630 (F); Ciénega "3 de Junio," at km 73 SE of San José on Carretera Panamericana, *Jiménez M.* 1993 (F, NY), *Jiménez M.* 3372 (F), *Lent* 405 (NY), and *Anderson & Mori* 231 (BM, DS, F, WIS); near Ojo de Agua, *Williams et al.* 28281 (BM, F, WIS); La Trinidad, between km 60 and 77, *Molina R. et al.* 17855 (F, GH). Border of Cartago and San José: Cerro de la Muerte, *Heithaus* 318 (MO). San José: Cerro de Buena Vista, *Tonduz (Pittier exped.)* 3498 (US); Cerro de las Vueltas, *Standley & Valerio* 43640 (F, US). PANAMA: Chiriquí: between Cerro Bine and Itamut, *Weston* 10175 (MO; first report of *Gentiana* in Panama).

In Central America, *G. sedifolia* is known only from high elevations in the Cordillera de Talamanca in Costa Rica and the adjacent Cordillera Central in Panama (Fig. 20). It is widely distributed in the Andes of South America, from Colombia and Ecuador south at least to the Cordillera Central of southern Peru (Fig. 21).

Herbarium data indicate that *G. sedifolia* in Costa Rica and Panama grows in boggy depressions and similar wet sites in meadows from 2275 to 3335 m elevation. Plants have been collected in flower from December through July.

In their original description of *G. sedifolia*, Humboldt et al. (1819) reported having seen this species "in montibus ignivomis Antisanæ [Ecuador], Puracé, Páramo de Almaguer [Colombia], etc., alt. 1600–1800 hex. [= 3072–3456 m]." On the basis of minor geographic variations in this species, discussed below, it seems most likely that the type was collected on or near Antisana.

Distinctive vegetative features of *G. sedifolia* throughout its range include the proportionately long-tapering leaves and the very narrow white margins. Distinctive floral features include the funnellform corolla tube, which widens more conspicuously from base to summit than the nearly cylindrical corolla tubes of the other species described here, and the relatively low divergence and long free portions of the filaments. Pollen grains of *G. sedifolia* from Costa Rica closely resemble those of Ecuadorean specimens, the sexine in both being relatively coarsely reticulate, with poorly developed longitudinal striations.

The two later species names cited above have generally been accepted as synonyms of *G. sedifolia*, at least the first having been based on the same collection (Humboldt et al., 1823). Ten taxa, with 11 epithets, were described as varieties, subvarieties, or forms of *G. sedifolia* during the 19th Century, but, except for the two cited above, their names seem to have been based on specimens of other species. Because all of these names were based on South American plants, a thorough investigation of their status has not

been included in this study. More recent collections, however, have indicated that much of the variation in *G. sedifolia* occurs within populations. Conspicuous variation exists in stem and internode length, but extremes can be found within a single population and even within a single collection, e.g., *Coubouy in 1855* (GH), from Ecuador, and *Pennell & Hazen 9996* (GH), from Colombia; some variation may occur among the stems of an individual plant. This variation, appearing to represent responses to seasonal factors and differences in microhabitat, is not recognized taxonomically here. Maximum flower size is greater in Ecuador than farther north, but there is considerable variation in all regions and no discontinuities are evident. Corolla color likewise varies within populations.

Plants of *G. sedifolia* from the region of Antisana and Cotopaxi in Ecuador often have relatively long, much-branched prostrate stem bases, which appear brownish-black from the remains of old leaf bases, and from which adventitious roots arise. Such plants resemble the type collection and appear to be long-lived and probably recurrently flowering, corresponding to the description of *G. sedifolia* as perennial by Humboldt et al. (1819). Plants from other parts of the range of *G. sedifolia* generally have less well developed prostrate stems, without blackish leaf remnants, and root systems comprising only the primary root and its branches. These plants appear to be relatively short-lived and monocarpic. Longevity and life cycles are, however, difficult to determine in specimens from the tropics, and no year-round observations have been made on populations of this species. Therefore it is not certain whether these differences represent genetic differentiation, or whether climatic conditions near the Equator permit greater longevity of individual plants. Weberbauer (in Gilg, 1906), however, commented on the inadequacy of plant size and apparent longevity as bases for dividing *G. sedifolia*, noting that at a single locality in Peru plants of this species might exhibit all stages of intergradation from minute, unbranched, one-flowered forms with a single filiform root to large, much-branched, patch-forming plants. Therefore no variants based on apparent longevity are recognized here.

2. *GENTIANA beamanii* Pringle, sp. nov. Figs. 2, 9, 15.

Caulis plus minusve erecti, 3.5–16 cm alti, internodiis vulgo longioribus quam foliis. Folia oblanceolata vel anguste spatulata, 5–10 mm longa, 1.5–2 mm lata, proximale fere ascendente et distale patente, marginibus albis usque ad 0.05 mm latis, apicem versus minute denticulatis. Tubus calycis 5–8 mm longus. Lobi calycis triangulares, 1.8–3 mm longi, acuti, marginibus albis circa 0.15 mm latis. Tubus corollae cylindricus, 8.5–14 mm longus. Lobi corollae late ovato-triangulares 1.5–3 mm longi, subacuti, indici. Partes librae plicarum triangulares, eroso-serratae et emarginatae, breviores quam lobi. Filamenta staminum sese liberantia aliquantum supra medium corollae totae, partibus libris antheribus inclusis circa 2.5 mm longis. Pollinis grana subprolata vel prolata, sexinio striato-reticulato. Capsula 4–6 mm longa, in parte exserta.

Type: GUATEMALA: Huehuetenango: Sierra de los Cuchumatanes, immediately N of Tojiah [Tojiquiá] at km 322 on Ruta Nacional 9N, *Beaman* 3899, 1 Aug 1960 (holotype MSC, isotypes GH, US). Paratypes: GUATEMALA: Huehuetenango:

vicinity of Chémal [Xémal], Sierra de los Cuchumatanes, *Steyermark* 50287, 8 Aug 1942 (F, GH).

Plants 3.5–16 cm tall. Stems more or less erect throughout or basally decumbent, usually 1–6, each usually with 1–3 branches arising in basal half and reaching about equal height, sometimes with additional branches from upper axils. Leaves usually broader and more closely spaced near stem base; lowest leaves (sometimes shriveled at flowering time) elliptic-oblong or oblanceolate, 5–15 mm long, 1.8–4 mm wide, spreading or ascending, scarcely conduplicate. Median and upper cauline leaves oblanceolate to narrowly spatulate, 5–10 mm long, 1.5–2 mm wide, increasingly conduplicate upward; proximal portions (ca. 1/3 near middle of stem, ca. 2/3 near summit) appressed-ascending, distal portions more or less arcuate-spreading. Leaf apices abruptly acuminate, apiculate. White leaf margins almost obsolete proximally, widening distally to ca. 0.08 mm, entire or sparsely and minutely undulate-denticulate above middle. Midrib keel of similar width, minutely denticulate above middle. Internodes distinct, all but lowest few usually 1–2.5 times as long as subtending leaves. Calyx tube 5–8 mm long, slightly ridged along midveins. Calyx lobes triangular, 1.8–3 mm long, acute to acuminate, scarcely to moderately conduplicate, erect or slightly arcuate-spreading distally, with white margins ca. 0.15 mm wide, entire or nearly so, and keel up to ca. 0.08 mm wide, entire or sparingly denticulate. Corollas 10–17 mm long when closed; expanded limb 6.5–12 mm across. Corolla tube 8.5–14 mm long. Lobes broadly ovate-triangular, 1.5–3 mm long, slightly wider than long, subacute to acute. Free portions of appendages ca. 0.8 times as long and about as wide as lobes, triangular, sparingly erose-serrate, usually emarginate to shallowly bifid. Corolla tube mostly whitish, blue above, with dark purple streaks on interior surface of throat, in 2 lines in each petal proper and 1 in each appendage; lobes and free portions of appendages medium blue; exterior surface with deep violet pigment between relatively pale margin and overlapping edge (when closed) of next lobe, giving striped appearance. Filaments becoming free slightly above 1/2 total height of corolla; free portions (including anthers) ca. 2.5 mm long. Pollen grains subprolate to prolate. Sexine relatively finely striato-reticulate. Pistil tapering into style ca. 1 mm long. Capsule 4–6 mm long, about 2/3 exerted from marcescent corolla by gynophore 7–10 mm long at maturity. Seeds not seen.

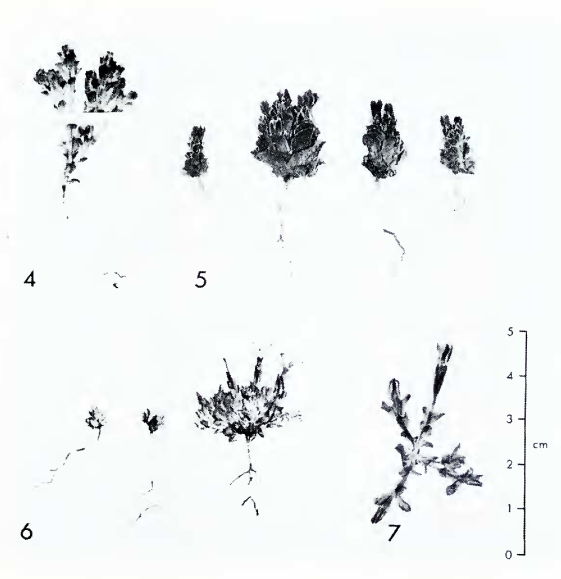
Gentiana beamanii is known only from a small area in Los Altos Cuchumatanes, Guatemala (Fig. 23). Both collections cited were made along small streams in meadows at altitudes of 3200–3750 m.

This species is named for Dr. John H. Beaman, author of several papers on the alpine flora of Mexico and Guatemala, whose notes and comments on differences among the Central American species of sect. *Chondrophyllae* have been very helpful in this study.

The elongate, erect stems and widely separated leaves of *G. beamanii* give this species an aspect unique among Central American species of sect.

Chondrophyllae. Its distinctness from plants treated here as *G. fieldiana* was first noted by Steyermark (in sched., *Steyermark* 50287), as follows: "Corolla larger, broader, and with longer tube . . . corolla-lobes with deeper purple in outer lobes [sic] . . . also stems with more branching and with more flowers than in other smaller type." Beaman (unpublished notes) likewise contrasted these plants, noting that those here called *G. beamanii* had narrower leaves with less conspicuous white margins.

Of the three Guatemalan species, *G. beamanii* is the closest to *G. sedifolia* in floral morphology. It differs conspicuously, however, in its cylindric, abruptly flaring corolla tube and in the much greater adnation of its stamens.



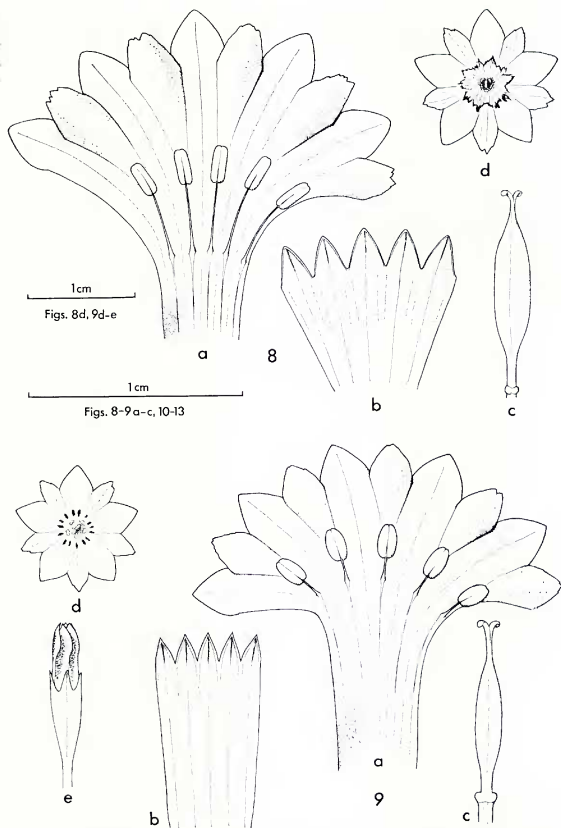
Figs. 4-7. Herbarium specimens of *Gentiana* spp. Fig. 4. *G. fieldiana* (Beaman 3071, MSC, a plant ca. average size). Fig. 5. *G. pumilio* (Matuda 2868, HAM) Fig. 6. *G. perpusilla* (Pringle 1749, HAM). Fig. 7. *G. prostrata* (Shacklette 6013, MICH, from Colorado). Figs. 1-7 to same scale.

3. *GENTIANA fieldiana* Pringle, sp. nov. Figs. 3, 4, 10, 16.

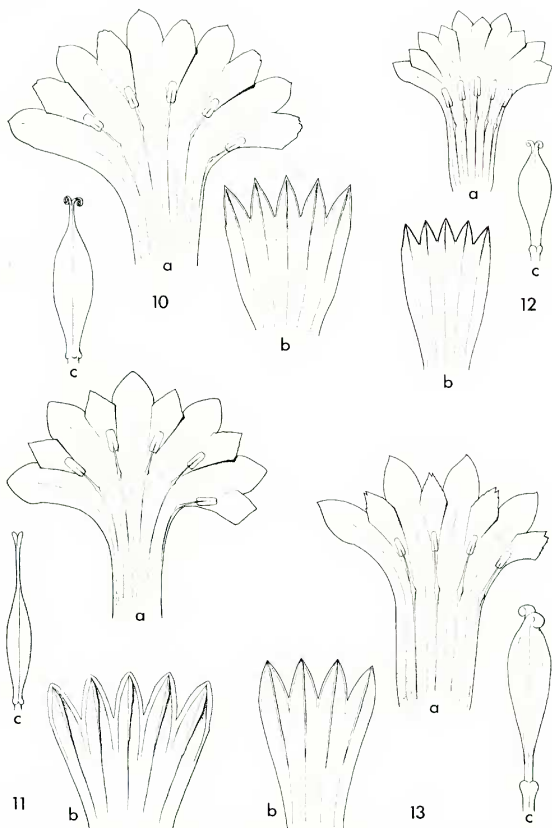
Caules ascendentes vel erecti, 1-4(-6.5) cm alti, vulgo pauciramosi. Folia congesta. Folia basalia oblongo-oblanccolata vel elliptico-obovata, 4-9 mm longa et 2-4 mm lata. Folia supera angustiora, marginibus albis carinisque circa 0.05 mm latis, apicem versus minute denticulatis. Tubus calycis 5-8 mm longus. Lobi calycis triangulares, acuminati, marginibus albis circa 0.05 mm latis, integris. Tubus corollae cylindricus, 4.5-10 mm longus. Lobi corollae oblongo-triangulares, 1.5-2 mm longi, apiculata, azurci aut albi. Partes librae plicarum triangulares, erose-serratae et vulgo emarginatae, breviores quam lobi. Filamenta staminum sese liberantia circa medium corollae totae, partibus libris antheribus inclusis circa 2 mm longis. Pollinis grana prolata, sexinio striato-reticulato. Capsula 3-5 mm longa, in parte vel in toto exserta.

Type: GUATEMALA: Huchuetenango: Chémal [Xémal], at km 318 on Ruta Nacional 9N, *Beaman* 3071, 4 Aug 1959 (holotype MSC). Paratypes: GUATEMALA: Huchuetenango (all from Los Altos Cuchumatanes): vicinity of Tunimá [Tunimá], *Steyermark* 48368, 7 Jul 1942 (F, GH); 2.5 mi E of San Mateo Ixtatán, *Steyermark* 49875, 31 Jul 1942 (F); near Páquix, *Sharp* 451025, 24 Dec 1945 (F, TENN); E of Tocquín [Tojquiá], *Holdridge* 2345, 27 Apr 1948 (US); Llano de Tierra Blanca, near trail to Todos Santos from Llano de San Miguel, near Chémal [Xémal], ca. 5 km W of km 311 on Ruta Nacional 9N, *Beaman* 3118, 5 Aug 1959 (MSC); 3 km S of road between Llano de San Miguel and Todos Santos, from a point 2.5 mi W of Llano de San Miguel, *Beaman* 3975, 2 Aug 1960 (MSC); 7 mi N of Santa Eulalia along road to San Mateo Ixtatán, *Breedlove* 8596, 5 Feb 1965 (F); along road to San Pedro Soloma, 3 mi SW of San Mateo Ixtatán, *Breedlove* 8637, 6 Sep 1965 (F, US). Totonicapán: near Cumbre del Aire, on road between Huchuetenango and Siga, *Standley* 65939, 20 Feb 1939 (F); Tecum Umán Ridge at km 154 on Ruta Nacional No. 1, ca. 20 km of Totonicapán, *Beaman* 4205, 14 Aug 1960 (MSC).

Plants 1-4(-6.5) cm tall. Stems 1-12, ascending to erect, those of larger plants usually with 1-4 branches at various levels and further branched near summit, bearing flowers in small, leafy cymes. Basal leaves (sometimes more or less marcescent at flowering time) spreading, scarcely conduplicate, with midrib keel well developed only near apex, broadly oblong-oblanccolate to elliptic-obovate, usually 4-9 mm long, 2-4 mm wide. Cauline leaves somewhat narrower, increasingly conduplicate and carinate upward; upper ones carinate for most of length. Leaf apices acute, apiculate. White leaf margins and keel sharply defined, both 0.05-0.13(-0.2) mm wide, or slightly wider toward apex, at least upper leaves with keel and usually margins minutely denticulate. Leaves of most plants densely crowded throughout; those of taller plants often more distant on lower part of stem, with lower internodes up to twice as long as subtending leaves, but crowded on upper part. Calyx tube 5-8 mm long. Calyx lobes triangular, 1-1.5 mm long, erect, scarcely conduplicate, acute to acuminate, with white margins ca. 0.05 mm wide, entire, and keels scarcely developed or up to 0.04 mm wide. Corollas 6-12 mm long when closed; expanded limb 5-8 mm across. Corolla tube 4.5-10 mm long. Lobes oblong-triangular, 1.5-2 mm long, apiculate. Free portions of appendages ca. 0.75 times as long and about as wide as lobes, triangular, erose-serrate, sometimes emarginate. Corolla tube mostly whitish; lobes, free



Figs. 8-9. *Gentiana* spp. Fig. 8. *G. sedifolia*. Fig. 9. *G. beamanii*. a, interior surface of corolla, slit longitudinally and pressed; b, exterior surface of calyx; c, pistil; d, intact open flower from above; e, closed flower.



Figs. 10–13. *Gentiana* spp. Fig. 10. *G. fieldiana*. Fig. 11. *G. pumilio*. Fig. 12. *G. perpusilla*. Fig. 13. *G. prostrata* (drawn from a specimen from Colorado, where this species normally bears tetramerous flowers). a, interior surface of corolla, slit longitudinally and pressed; b, exterior surface of calyx; c, pistil.

portions of appendages, and uppermost portion of tube white to medium blue; exterior surface of lobes, except near margins, suffused with green, and occasionally also with deep violet-blue except near inner margin. Stamens becoming free at ca. 1/2 total length of corolla; free portions (including anthers) ca. 2 mm long. Pollen grains prolate. Sexine relatively coarsely striato-reticulate. Pistil tapering into style ca. 1 mm long. Capsule 3-5 mm long, 2/3 to entire length and up to 2 mm of gynophore exerted from marcescent corolla at maturity. Seeds ellipsoid, light brown, striato-reticulate, ca. 0.7 mm long, 0.35 mm in diameter.

Gentiana fieldiana is native to the Sierra Madre and Los Altos Cuchumatanes in Guatemala (Fig. 22) where it grows in moist sites in subalpine meadows (llanos) and openings in pine forests, from 2500 to 3500 m. Plants have been collected in flower from December through July. Its name honors the contributions of botanists now and formerly of the Field Museum of Natural History to the knowledge of the flora of Guatemala, especially Dr. Julian A. Steyermark and the late Mr. Paul C. Standley, who first collected this species.

A conspicuous feature of all but the smallest plants of *G. fieldiana* is the presence of 1-several short, leafy branches near the summit of the stem, with the flowers thus being borne in small cymes. In this trait, *G. fieldiana* differs from *G. sedifolia*, *G. beamanii*, and *G. prostrata*, in all of which solitary flowers generally terminate longer branches or unbranched stems (one such branch occasionally present in *G. sedifolia*). Also, *G. fieldiana* differs from the other species discussed here in that its corolla lobes taper abruptly to an apiculate tip, rather than gradually from near the base. Its pollen is similar to that of *G. sedifolia*, but the sexine pattern is more distinctly striato-reticulate, rather than simply reticulate, and the lirae are finer.

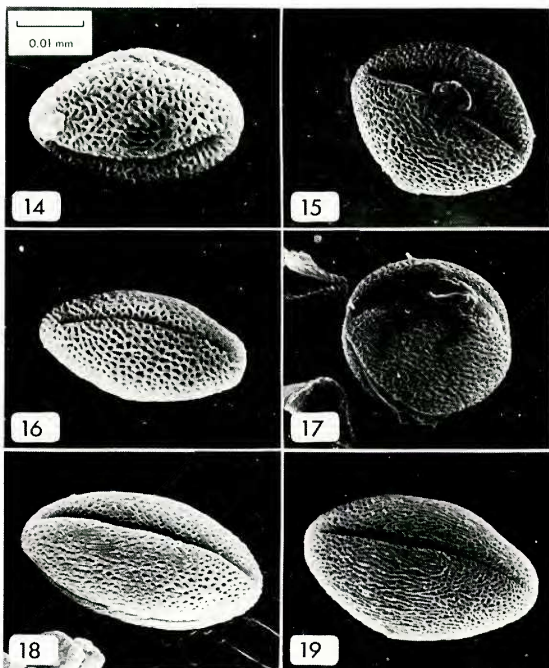
Photographs of living plants of *G. fieldiana* were not available for this study, but *Breedlove* 8637 and *Sharp* 451025 contain some corollas pressed while open, with the colors well retained. From these specimens it appears that no guidelines or sharply contrasting corolla-throat patterns are present in this species.

Some specimens of *G. fieldiana* were previously identified as *G. pumilio*. Both of these species, as well as *G. beamanii*, have been collected near Xémal, but even in this area they maintain their distinctness. *Gentiana fieldiana* is readily distinguishable from *G. pumilio* by its narrower, less densely crowded leaves with narrower, less prominently denticulate margins, and by the shape of its corolla lobes.

Breedlove 8596 consists of usually large plants with relatively narrow leaves for this species. The general aspect of these plants consequently resembles that of *G. sedifolia*, but their well-developed leaf margins and keels and the position of their stamens clearly identify them as *G. fieldiana*.

4. GENTIANA PUMILIO Standl. & Steyer., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:76. 1944. Type: GUATEMALA: San Marcos: between San Sebas-

tián and summit of Volcán de Tajumulco, *Steyermark* 35489, Feb 1940 (holotype F!, isotypes MSC!). Figs. 5, 11, 17.



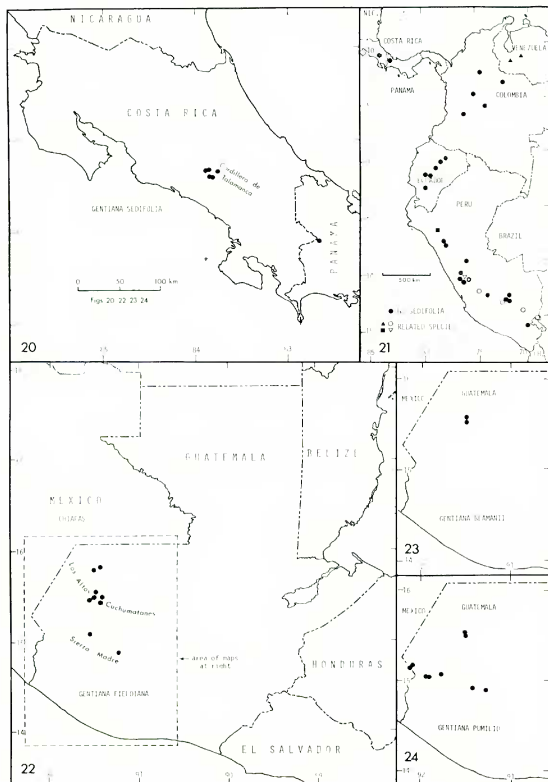
Figs. 14–19. Scanning-electron photomicrographs of pollen grains of *Gentiana* spp. Fig. 14. *G. sedifolia* (Mulroy 1099, HAM). Fig. 15. *G. beamanii* (Beaman 3899, MSC). Fig. 16. *G. fieldiana* (Beaman 3071, MSC). Fig. 17. *G. pumilio* (Matuda 2868, MSC). Fig. 18. *G. perpusilla* (Rzedowski 25681, MICH). Fig. 19. *G. prostrata* (Sharp s.n., HAM, from Alaska). Figs. 14–19 to same scale.

Plants 0.7–4 cm tall. Stems usually 1–10, sometimes much branched forming dense tufts. Basal and lower cauline leaves persistent and green or the lowest pairs marcescent. Leaves ascending, densely imbricate-crowded on whole length of stem, broadly spatulate to orbicular, either tapering gradually to base or at least upper leaves more commonly abruptly contracted below middle. Larger, lower leaves 2.5–15 mm long, 0.3–1.2 times as wide as long; upper leaves smaller and more strongly ascending but similar in proportions. Apices abruptly acuminate-apiculate. All leaves prominently white-margined and keeled but not strongly conduplicate; margins and keels of upper leaves mostly 0.25–0.35 mm wide, minutely but copiously denticulate at least above middle. Flowers solitary or in clusters of 2–3. Calyx tube largely concealed by leaves, 3–5.5 mm long, carinate distally. Calyx lobes ovate-triangular, erect, strongly carinate-conduplicate, 1–2.3 mm long, 0.5–1.5 mm wide, obtuse, with prominent white margins and keels ca. 0.2 mm wide, denticulate to base. Corollas 5–11 mm long when closed; expanded limb 4–7 mm across. Corolla tube 4–9 mm long. Lobes ovate-triangular, 1–2 mm long, ca. 1.2 times as wide as long, obtuse. Free portions of appendages triangular, ca. 0.6 times as long and 0.8 times as wide as lobes, acute, entire or shallowly undulate. Corolla tube mostly greenish-white; lobes, free portions of appendages, and upper part of tube white to light blue; exterior surface of petals proper moderately to strongly suffused with green, and in blue corollas sometimes with deep violet, the suffusion strongest toward center. Stamens becoming free at ca. 3/5 total height of corolla; free portions (including anthers) ca. 2.2 mm long. Pollen grains spheroidal. Sexine relatively fine striato-reticulate. Style ca. 3 mm long, spiralling in fruit. Capsule 5–7 mm long, 1/2 to almost completely exerted from marcescent corolla. Seeds cylindrical-ellipsoid, medium brown, striato-reticulate, ca. 0.9 mm long and 0.3 mm in diameter.

Additional specimens examined:

GUATEMALA: Huehuetenango (all from Los Altos Cuchumatanes): region of Chémal [Xémal], *Standley 81107* (F); cumbre de la Sierra de los Cuchumatanes, between the first cumbre and La Pradera, *Standley 81172* (F); near Calaveras, *Williams et al. 21954* (F) and *21955* (F, NY, US); 3–15 km N of Chémal [Xémal], *Williams et al. 22208* (F). San Marcos: between Sibinal and summit of Volcán Tacaná, *Steyermark 36156* (F); Volcán Tajumulco, *Bunting 337* (F); between Comitancito [Comitancillo] and Santa Rosa junction, Sierra Madre, *Williams et al. 27058* (F); lower slopes of Volcán Tajumulco near San Sebastián, *Plouman 3064* (GH). Sololá: near María Tecún, Sierra Madre, about 10–12 km NW of Los Encuentros, *Williams et al. 27325* (F). Totonicapán: region of Desconsuelo, *Standley 62735* (F); region of Salvachán, mountains above Totonicapán, just before reaching Desconsuelo, *Standley 84489* (F); slopes of María Tecún above Totonicapán, *Williams & Williams 18557* (GH, US); summit of Cerro María Tecún, about 12 km SW of Totonicapán, *Williams et al. 25457* (F); María Tecún, *Molina R. et al. 16376* (F, NY, US). MEXICO: Chiapas: Volcán de Tacaná pico, *Matuda 2868* (F, GH, HAM, K, MEXU, MICH, MSC, NY, US).

Gentiana pumilio is native to the Sierra Madre of southwestern Guatemala



Figs. 20-24. Documented distribution of *Gentiana* spp.

and adjacent Chiapas, Mexico, and to Los Altos Cuchumantanes in Guatemala. All collections of this species are from open habitats, mostly in subalpine or alpine zones, from ca. 2500 to 4062 m. Most collections are from moist sites, but some are from dry slopes and pastures. Plants have been collected in flower from November through May.

Because of its proportionately wide leaves and the wide and conspicuous white margins and keels of its leaves and calyx lobes, *G. pumilio* is readily distinguishable from the other species described here. Its relatively long style and spheroidal pollen grains are also distinctive. *Gentiana pumilio* further differs from the three preceding species in that the flowers are often borne in clusters of two or three, rather than singly at the ends of branches.

5. *GENTIANA PERPUSILLA* Brandege, *Zoe* 5:181. 1904. Type: MEXICO: México: Ixtacchiuatl, *Purpus* 302, Mar-Jul 1903 (holotype US!, isotypes F!, GH!, MO!, MSC!, UC). Figs. 6, 12, 18.

Plants 0.8–3 cm tall. Stems 1–10, ascending, not branched except occasionally near base. Leaves short-acuminate, apiculate. Basal leaves mostly in good condition at flowering time, obovate to broadly spatulate, moderately ascending, scarcely to moderately conduplicate, 4–10 mm long, 1.8–3.5 mm wide. Cauline leaves densely crowded, increasingly conduplicate and more strongly ascending upward, those near summit of stem oblanceolate, 3–6 mm long, 1–2.5 mm wide. White leaf margins and midrib keel inconspicuous, ca. 0.05 mm wide, entire or with a few shallow projections near apex. Calyx tube 4–6.5 mm long, carinate distally. Calyx lobes triangular, erect, 1–1.2 mm long, 0.7–1 mm wide, acute, with white margins and keels ca. 0.08 mm wide, entire. Corollas 5–9.5 mm long when closed; expanded limb 3.5–4.5 mm across. Corolla tube 4–8.5 mm long. Lobes ovate-triangular, 1–2 mm long, about as wide as long, subacute. Free portions of appendages triangular, ca. 0.67 times as long and about as wide as lobes, subacute to acute, entire, merely undulate, or shallowly few-toothed. Corolla tube mostly greenish-white; lobes and free portions of appendages pale to medium blue; exterior surface of lobes, except near margins, and adjacent portions of tube strongly suffused with green. Stamens becoming free at ca. 2/3 total height of corolla; free portions (including anthers) 1.5–2 mm long. Pollen grains prolate. Sexine relatively finely striato-reticulate. Style almost obsolete. Capsule 2.5–3.5 mm long, 1/2 to entire length and up to 3 mm of gynophore exerted from marcescent corolla. Seeds ovoid-ellipsoid, brownish-white, striato-reticulate, ca. 0.75 mm long, 0.5 mm in diameter.

Additional specimens examined:

MEXICO: México (all from the SW side of Ixtacchiuatl): Cañada de Alcalican (Tlaltapitongo) below La Joya, *Beaman* 3534 (MSC); La Joya, Cañada de Alcalican, *Rzedowski* 21594 (ENCB) and 25681 (ENCB, MICH, MSC); in canyon below end of auto road, ca. 2.4 km N of microwave tower, *J.S. Pringle* 1749 (HAM). Veracruz: Cofre de Perote, NW side of mtn., *Beaman* 2197 (GH, MSC).

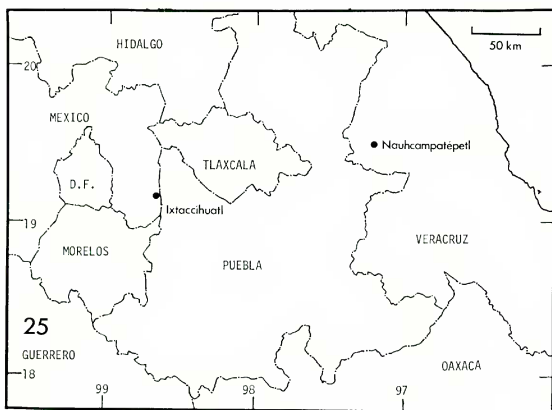


Fig. 25. Documented distribution of *Gentiana perpusilla*.

The two localities known for *G. perpusilla* are on peaks in the Transverse Volcanic Zone of Mexico (Fig. 25). It grows in the alpine zone at ca. 3850 m on Ixtaccihuatl and 3590 on Nauhcampatépétl (Cofre de Perote), in microhabitats that are wet at least in summer.

Among the species described here, *G. perpusilla* has by far the smallest corollas, and its pollination appears probably to be largely hydrocleistogamous. It grows where fog and drizzle are nearly continuous during its flowering season, and consequently its photonastic corollas are infrequently and briefly open. Observation of pollen in preserved flowers from Ixtaccihuatl indicated that dehiscence of the anthers into the small space within a closed corolla can readily bring pollen into contact with the stigmatic lobes. In one corolla, however, the presence of a few alien grains indicated that some chasmogamous pollination does occur.

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